PB81-165854

The Comparative Photobehavior of Laboratory-Hatched and Plankton-Caught 'Balanus Improvisus' (Darwin) Nauplii and the Effects of 24-Hour Starvation

(U.S.) Environmental Research Lab.
Narragansett, RI

Mar 81

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1. REPORT NO. EPA-600/J-80-229	2. Journal Article	3. RECI PB81-165854
4. TITLE AND SUBTITLE The Comparative Photobehavior of Laboratory-Hatched and Plankton-Caught Balanus improvisus (Darwin) Nauplii and the Effects of 24-Hour Starvation		5. REPORT DATE March 1981 6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) William H. Lang, Martha Marcy, Patricia J. Clem, Don C. Miller and Michael R. Rodelli		8. PERFORMING ORGANIZATION REPORT NO. ERLN-J136
9. PERFORMING ORGANIZATION NAME AND ADDRESS		10. PROGRAM ELEMENT NO. AAKN1C 11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS Environmental Research Laboratory - Narragansett, RI Office of Research and Development U.S. Environmental Protection Agency Narragansett, Rhode Island 02882		13. TYPE OF REPORT AND PERIOD COVERED Journal Article 14. SPONSORING AGENCY CODE EPA/600/05

15. SUPPLEMENTARY NOTES

ERLN-J136 J. exp. mar. Biol. Ecol.

16. ABSTRACT

Stage II nauplii of Balanus improvisus (Darwin) were obtained from laboratory-maintained adult barnacles. The immediate phototactic and photokinetic response of laboratory nauplii to light stimuli of known wavelength (460-540 nm) and quantal intensity was determined through use of closed-circuit videotape recordings quantified for computer analysis. Spectral and light intensity responses were compared with previous results using nauplii collected from the plankton. In both cases, nauplii exhibit a primary peak response to light near 480 nm and a secondary peak near 520 nm. Although the spectral response and basic patterns of photobehavior remain similar in field and laboratory nauplii, sensitivity to light intensity is significantly reduced in laboratory nauplii. Responses of fed and 24-h starved laboratory nauplii were also compared at three salinities (15, 20, 30°/oo). Starvation for 24 h, although inducing no major change in photopositive and photokinetic response of nauplii, can slightly depress spontaneous swimming speed and raise the threshold of intensity response for phototaxis.

different

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

PRODUCT OF:
NATIONAL TECHNICAL INFORMATION SERVICE
U.S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

18. DISTRIBUTION STATEMENT	19. SECURITY CLASS *(This Report)*	21. NO. OF PAGES
RELEASE TO PUBLIC	UNCLASSIFIED	
	20. SECURITY CLASS *(This page)*	22. PRICE
	UNCLASSIFIED	

EPA Form 2220-1 (9-73)

TABLE II

Mean linear velocity (MLV) in mm/sec and *t*-test significances for fed versus 24-h starved stage II *Balanus improvisus* nauplii: details of MLV determination and sample numbers are given in Table I; results of Pearson product–moment correlations (p–m corr.) appear at the bottom of each MLV column; +, direct relationship between MLV and light intensity; ○, no relationship between MLV and light intensity ($P > 0.05$).

Intensity (W/m^2)	*S*, 20‰ MLV Fed	*S*, 20‰ MLV Starved	*S*, 20‰ Sig. (0.05)	*S*, 30‰ MLV Fed	*S*, 30‰ MLV Starved	*S*, 30‰ Sig. (0.05)
Dark-adapted						
2.5	1.98	1.70	No	1.84	1.75	No
10^{-1}	1.87	1.93	No	2.01	2.02	No
10^{-2}	1.82	1.78	No	2.04	2.08	No
10^{-3}	2.05	1.54	Yes	1.82	1.54	Yes
10^{-4}	1.57	1.39	No	2.05	1.49	Yes
10^{-5}	1.62	1.70	No	1.83	1.50	Yes
Cont.	1.62	1.69	No	1.81	1.43	Yes
p–m corr.	+	0		0	+	
Light-adapted						
4.0	2.47	2.51	No	1.61	2.00	Yes
10^{-1}	1.70	2.44	Yes	1.54	1.55	No
10^{-2}	1.80	1.47	Yes	1.29	1.13	Yes
10^{-3}	1.52	1.23	No	1.15	1.13	No
10^{-4}	1.51	1.26	No	1.26	1.22	No
10^{-5}	1.54	1.53	No	1.16	1.20	No
Cont.	1.64	1.25	Yes	1.38	1.24	No
p–m corr.	+	+		+	+	

TABLE III

Mean linear velocity (MLV), χ^2 comparison of directional orientation, and *t*-test comparison (MLV comp.) of stage II *Balanus improvisus* nauplii responding to a 3.5-sec 480-nm light stimulus at different intensities: nauplii are dark-adapted at 20 °C, 15‰ *S*; *, significant ($P \leq 0.05$) non-random directional responses; see Table I for further explanation of χ^2 and subset tests; the MLV of fed and 24-h starved nauplii are compared using a *t*-test (see Table II).

Intensity (W/m^2)	Fed *n*	Fed χ^2	Fed MLV (mm/sec)	Fed Subset	Starved *n*	Starved χ^2	Starved MLV (mm/sec)	Starved Subset	MLV comp. Sig. (0.05)
0.25	37	16.0*	1.75	AB	51	51.5*	1.56	A	No
10^{-2}	41	80.0*	1.94	A	57	113.4*	1.56	A	Yes
10^{-3}	50	98.1*	1.55	B	24	53.5*	1.24	B	Yes
10^{-4}	42	45.1*	1.54	B	31	19.9*	1.05	BC	Yes
10^{-5}	53	9.2	1.23	C	32	6.2	0.92	C	Yes
10^{-6}	46	9.3	1.04	C	38	5.3	0.87	C	Yes
10^{-7}	42	5.4	1.15	C	42	9.1	0.99	BC	Yes
Cont.	48	2.8	1.10	C	60	4.8	0.89	C	Yes

tensities (Table I). A direct correlation between increasing MLV and increasing light intensity for light-adapted nauplii was statistically substantiated (Table II).

Fed dark-adapted laboratory nauplii show maximal MLV at intermediate light intensities (Tables I, III). The change in MLV, however, is not statistically significant for nauplii at 30‰ *S* (Table I). A significant decrease in MLV at the highest light intensity was not evident for nauplii at either 20‰ or 30‰ *S* (Table I), in contrast to results with field nauplii (Lang *et al.*, 1979a).

A comparison of the MLV of fed and starved test groups over a 3.5-sec interval of light stimulation or control conditions shows that in over 50% of the cases (19 of 36) no statistically significant (0.05 level) difference occurs (Tables II, III). Seventeen groups did show significant differences ($P < 0.05$), with the starved nauplii having a reduced MLV in 15 of the 17 cases. In two cases, starvation enhanced MLV in light-adapted nauplii during response to higher light intensity stimuli. Starvation may, in some cases, depress MLV of nauplii, but does not impair an immediate photokinetic response. Overall, the impact of 24-h starvation on stage II naupliar photoresponse appears marginal.

Discussion

In view of the time, effort, and logistical requirements involved in collecting and sorting live plankton samples, laboratory-hatched nauplii represent a decidedly more practical means of obtaining study material. This investigation has attempted to study some aspects of the reliability of using laboratory nauplii to evaluate behavior of natural populations.

For the 24-h period prior to testing, laboratory and field nauplii were subjected to similar laboratory conditions. However, essential differences still exist between the two groups. Plankton-caught test groups represent far more heterogeneous samples both in terms of origin and age of larvae. Field nauplii had experienced natural variations of physical parameters and exposure to temperatures below 15 °C (Lang *et al.*, 1979a). In contrast, laboratory nauplii represent relatively homogeneous samples, with a given test group originating from one or perhaps two adults held at relatively constant laboratory conditions of temperature (20 °C), salinity (15, 20 or 30‰), and artificial light. Furthermore, all laboratory nauplii hatched within a 6- to 8-h time period and represent a uniform age group.

The results of spectral response of laboratory nauplii to 460–540 nm light indicate a decline in sensitivity at 500 nm relative to response at 480 and 520 nm. These responses are in agreement with the spectral response curve generated for field nauplii (Lang *et al.*, 1979, Fig. 6), where the maximal sensitivity is at 480 nm with a possible secondary peak at 520 nm.

Although spectral response of laboratory and field nauplii appears similar, some aspects of intensity sensitivity at 480 nm differ. The percent of laboratory nauplii

exhibiting positive phototaxis at a given light intensity is often less than that observed in field nauplii. More importantly, laboratory nauplii consistently exhibit a higher threshold for significant response (Figs 2, 3), indicating decreased sensitivity relative to field nauplii.

The effect salinity plays on phototaxis and swimming activity of *Balanus improvisus* larvae is unclear. Sudden changes in salinity (± 10‰) will induce a temporary phototactic reversal to a negative response in stage II *B. improvisus* (per. obs.) and other cirriped species (Forward, 1976). Continuous exposure to different salinities may produce less obvious effects. Plankton-caught stage II nauplii tested at 30‰ *S* were more responsive to light relative to nauplii at 15‰ *S* (Lang *et al.*, 1979a) and appear to have a slightly increased spontaneous MLV (1.5 mm/sec at 15‰ *S*, 1.8 mm/sec at 30‰ *S*). Present results further indicate that spontaneous MLV may be affected by salinity. Three of four test groups at 20, and 30‰ *S* exhibited significantly increased control MLVs relative to nauplii at 15‰ *S* (Tables I, III).

For laboratory nauplii ≈ 24 h old, salinity appears to have no consistent effect on phototaxis. Nauplii at 20‰ *S* exhibit the highest percent phototactic response relative to those at 15, and 30‰ *S* (Fig. 2), but thresholds of significant response are nearly identical in all groups. Studies in progress, however, indicate that salinity-related differences in phototaxis may appear in older stage II and stage III nauplii (48–96 h).

Starvation for 24 h induces no *major* changes in the photobehavior of stage II laboratory nauplii. Studies rearing *B. improvisus* nauplii (Lang *et al.*, 1979b) also indicate that 24-h starvation does not impair development or increase mortality. Spontaneous swimming speeds of starved nauplii may decrease (Tables II, III) and phototaxis, in some cases, is depressed (Fig. 3). Differences in response of fed and starved nauplii showed no clear relationship to state of light-adaptation or salinity.

Singarajah *et al.* (1967) noted that starved nauplii of two barnacles species were less photonegative to a white-light stimulus relative to fed nauplii. A similar but not as marked effect was observed in present studies, but not consistently (Fig. 3). When a difference is seen, starved nauplii tend to be less sensitive to light. A net result of this may be that at higher light intensities, starved nauplii remain more photopositive (or less likely to turn away from the light) relative to fed nauplii. However, the present data do not suggest that nutritional state induces a significant direct effect on naupliar photoresponse as suggested by Singarajah *et al.* (1967). The subtle decline seen in MLV and photoresponse of starved nauplii may simply reflect a general deterioration in their physiological condition.

Laboratory-hatched nauplii tend to be less responsive and sensitive to 480 nm light than plankton-caught nauplii. The greater sensitivity of field nauplii may be a consequence of collection methods. For example, surface plankton tows may selectively capture only the more responsive, stronger swimming nauplii, while a laboratory test group represents a random sample of essentially all motile nauplii released by an adult. Other factors, such as the less uniform age distribution and

exposure to natural light in field nauplii, may also be important contributing factors.

For the parameters tested, the behavior of laboratory nauplii is adequately representative of field naupliar responses. Photobehavior studies, using laboratory-hatched barnacle nauplii, underestimated the light sensitivity observed in field nauplii, but significant differences in swimming behavior or phototaxis were not observed. Although substantial progress has been made in successful rearing of marine invertebrates, it is usually unknown if a laboratory larva retains physiological and behavioral parameters similar to its 'real world' counterpart. More studies are needed to answer this question.

Acknowledgements

We would like to thank S. Lawrence for her assistance in videotaping and D. J. Sleczkowski for many hours of essential work in computer operations and programming needs. We would also like to thank Drs R. B. Forward and G. Klein-MacPhee for critical reviews of the paper and numerous valuable suggestions.

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J. exp. mar. Biol. Ecol., 1980, Vol. 42, pp. 201–212
Elsevier/North-Holland Biomedical Press

EPA-600/J-80-229
Journal Article

THE COMPARATIVE PHOTOBEHAVIOR OF LABORATORY-HATCHED AND PLANKTON-CAUGHT *BALANUS IMPROVISUS* (Darwin) NAUPLII AND THE EFFECTS OF 24-HOUR STARVATION

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Abstract: Stage II nauplii of *Balanus improvisus* (Darwin) were obtained from laboratory-maintained adult barnacles. The immediate phototactic and photokinetic response of laboratory nauplii to light stimuli of known wavelength (460–540 nm) and quantal intensity was determined through use of closed-circuit videotape recordings quantified for computer analysis. Spectral and light intensity responses were compared with previous results using nauplii collected from the plankton. In both cases, nauplii exhibit a primary peak response to light near 480 nm and a secondary peak near 520 nm. Although the spectral response and basic patterns of photobehavior remain similar in field and laboratory nauplii, sensitivity to light intensity is significantly reduced in laboratory nauplii. Responses of fed and 24-h starved laboratory nauplii were also compared at three salinities (15, 20, 30‰). Starvation for 24 h, although inducing no major change in photopositive and photokinetic response of nauplii, can slightly depress spontaneous swimming speed and raise the threshold of intensity response for phototaxis.

INTRODUCTION

Light may act as an initiating, a controlling, and/or orienting cue in the vertical movement of zooplankton. In the case of benthic invertebrate larvae, positive phototaxis probably is an important factor in moving larvae toward surface waters (Thorson, 1964). Light has been also thought to play a primary role in the depth regulation of invertebrate larvae (Bousfield, 1955; Thorson, 1964). However, as light intensity represents a highly variable cue, responses to other stimuli, such as gravity and pressure, are now considered to be of equal or greater importance (Crisp, 1976; Burton, 1979). Although phototaxis is a pronounced and common response in barnacle and other invertebrate larvae, the functional significance of this response is not yet well understood.

Numerous qualitative studies on phototaxis of barnacle nauplii exist (Thorson, 1964), yet detailed quantitative studies are rare (Barnes & Klepal, 1972; Crisp & Ritz, 1973). We have initiated a series of studies to provide a rigorous analysis of the photobiology of barnacle larvae. The directional and kinetic response of *Balanus improvisus* nauplii to light spectrum and intensity were determined (Lang *et al.*, 1979a). Test larvae used were obtained directly from plankton samples. The present

study determines if stage II *B. improvisus* hatched from laboratory-maintained adult barnacles retain photobehavior comparable to plankton-caught (field) nauplii.

Barnacle nauplii (Singarajah *et al.*, 1967) and other zooplankton (Forward, 1976; Burton, 1979) are known to alter photoresponse with feeding. Changes in photobehavior in response to nutritional state has potential significance in models for plankton behavior (Forward, 1976). The effects of 24-h starvation on the swimming speed and phototaxis of laboratory hatched stage II nauplii has also been studied.

METHODS

EXPERIMENTAL ANIMALS

Adult *B. improvisus* were collected during July, 1978 and April, 1979 from shallow subtidal regions of Pettaquamscutt River near Narragansett, Rhode Island, U.S.A. Stones with numerous live barnacles were scrubbed clean of algae and debris and submerged in sea water of the appropriate salinity in 8-inch (20-cm) Carolina culture dishes. Sea water obtained from near the collection site at high tide (30‰ *S*) was filtered and portions diluted to 20 and 15‰ *S* with deionized water. The adult barnacles were maintained in cultures at 15, 20, and 30‰ *S* at 20 °C and constant illumination. Water in cultures was changed at 2- to 3-day intervals or after release of nauplii; adults were fed newly hatched *Artemia* nauplii (San Francisco Bay Brand[1]) and mixed-algal cultures.

Cultures were checked each morning for release of nauplii. If large numbers were evident, nauplii were pipetted into 0.45 μm filtered sea water at the same salinity as the adult culture. About 200 nauplii were then divided between plain filtered sea water or sea water with a mixture of *Isochrysis galbana* and *Tetraselmis suecia* added. These 'fed' and 'starved' groups were maintained overnight under constant illumination (single cool white 40 W fluorescent lights) at 20 °C. The starved groups were without food for 23.5 to 25 h before their photobehavior was recorded on videotape. All experiments were conducted between 11.00–16.00 h. Nauplii used in experiments were released from adult barnacles maintained from 10–30 days under laboratory conditions.

EXPERIMENTAL PROCEDURE

The directional and kinetic responses of test nauplii to a horizontal light stimulus were recorded on videotape. Video records were then computer analyzed using a video-to-digital processor interface called the 'Bugwatcher' (Wilson & Greaves, 1979).

[1] The Environmental Protection Agency does not approve, recommend or endorse any product mentioned in this publication.

For videotaping, replicate samples of about 30 nauplii each were transferred from 'fed' and 'starved' cultures to 3.5 × 3.5 × 2.0 cm rectangular lucite cuvettes. Dark-adapted nauplii were kept in a dark 20 °C temperature-controlled incubator for at least 1 h prior to videotaping; light-adapted nauplii were exposed to fluorescent lights supplemented at least 1 h with a 60 W incandescent bulb. Immediately before videotaping, water levels in cuvettes were adjusted to slightly less than 1.0 cm depth.

Videotaping was conducted in a temperature-controlled darkened room. A Wild M-5 dark-field base fitted with a 830 nm interference filter provided illumination for a Cohu-4400 television camera mounted overhead (Lang *et al.*, 1979b). Movement of nauplii was recorded in a horizontal field approximately 3 × 3 × 1 cm.

A light stimulus was applied horizontally to the cuvette. The xenon light source, monochromator, filters, and electromagnetic shutter are as described in Lang *et al.* (1979a).

Wavelength of the light stimulus was controlled by a combination of the monochromator and 3-cavity bandpass filters. Since previous results (Lang *et al.*, 1979a) indicated maximum response of stage II nauplii occurred between 480–520 nm, only wavelengths at 460, 480, 500, 520, and 540 nm (half bandwidth approximately 7 nm) were tested. Light intensity was regulated with neutral density filters.

Testing of naupliar light responses was conducted similar to previous experiments with plankton-caught nauplii (Lang *et al.*, 1979a). Light-adapted nauplii were transferred from temperature box to microscope stage under room lights; dark-adapted nauplii were transferred under dim deep-red light (≃ 700 nm). A cuvette of nauplii was aligned on the dark-field stage and all lights were extinguished for 30 sec to allow for dissipation of water movement before taping was begun.

For spectral response, one test group of nauplii was exposed in ascending order to seven intensities (≃ 10^{11}–10^{17} quanta/m^2 sec) of light stimuli at the test wavelength. A 1-min recovery period in total darkness was allowed between each stimulus. After one test series of seven intensities, the test group was replaced with fresh animals. From two to four replicates were tested at each wavelength (460, 480, 500, 520, 540 nm at 15‰ *S*; 480, 500, 520 nm at 20‰ *S*).

Additional intensity response experiments (480 nm), comparing fed and starved nauplii, were conducted in the same way; however, only six light intensities were tested.

Computer analysis, also described fully in Lang *et al.* (1979a), was used to determine mean linear velocity (MLV) and direction of travel (DOT) for each nauplius tracked on videotape. Videotapes were processed at 5 frames/sec. Hence, every 12th frame of the 60 frame/sec recording was digitized, resulting in a time series of *X*–*Y* coordinates (path) indicating displacement of nauplii at 0.2-sec intervals (Greaves, 1975).

Swimming speeds are presented as mean linear velocity for all test organisms during the full 3.5-sec light stimulus or, in the case of controls, the MLV during a 3.5-sec interval with 830 nm substage illumination only. Standard SAS programs –

Pearson product-moment correlation, General Linear Models, Duncan's multiple range test, *t*-test – were used for statistical analysis of MLV data (Barr *et al.*, 1976).

The mean angular direction of swimming (Batschelet, 1965) for each naupliar path was determined only during the last 2.5 sec of the 3.5-sec light stimulus. This 1-sec delay allows for an initial 'orientation period' in naupliar directional response (see Lang *et al.*, 1979a). Unless otherwise indicated (Fig. 3), directional responses are presented as percent distributions of the mean angular direction for all naupliar paths within a sample group using 60° directional intervals. A DOT mean $\pm 30°$ toward the light source is considered positive phototaxis. DOT distributions of experimental groups were tested against a theoretical uniform distribution using the χ^2 test (Batschelet, 1965).

In reporting and discussing results, the term 'response' denotes that nauplii exhibit phototaxis or photokinesis to a given light stimulus. Thus an 'increased response' infers that a greater percentage of nauplii exhibited a photoresponse. 'Sensitivity', on the other hand, is used specifically in reference to the threshold of significant phototaxis. 'Increased sensitivity' infers only that the threshold of statistically significant naupliar photoresponse has expanded and not necessarily that the general level of percent phototaxis also increased.

Results

Plankton-caught nauplii (15‰ *S*, 20 °C) tested from 440 to 640 nm at a constant quantal intensity of approximately 10^{15} quanta/m^2/sec had a peak spectral response from 480 to 520 nm (Lang *et al.*, 1979a). Testing of spectral response for laboratory-hatched nauplii was limited to a range of wavelengths from 460–540 nm; however, an action spectrum was tested (Fig. 1), as opposed to a response spectrum in the initial study (Lang *et al.*, 1979a).

At 15‰ *S* and 20 °C, laboratory-hatched nauplii are most sensitive to 480 nm light and exhibit a secondary peak at 520 nm (Fig. 2). Nauplii similarly tested at 20‰ *S*, 20 °C and 480, 500, and 520 nm light also exhibited a decline in sensitivity at 500 nm relative to responses at 480 and 520 nm (Fig. 1).

Although field and laboratory nauplii exhibit similar spectral responses, with peak sensitivity at or near 480 nm, a detailed comparison of intensity response at 480 nm shows significant differences. In Fig. 2, the intensity response of dark-adapted laboratory nauplii (15, 20, 30‰ *S*) and dark-adapted field nauplii (15‰ *S*) are compared. At 15‰ *S*, the percent of responding laboratory nauplii is reduced relative to field nauplii. Of more significance is a shift in sensitivity between the groups. Laboratory nauplii fail to exhibit a significant ($P > 0.05$) positive phototaxis at 10^{-5} W/m^2 in contrast to a significant response below 10^{-6} W/m^2 for field nauplii. Laboratory nauplii also maintain a strong phototaxis at higher light intensities (between 10^{-1} to 10^{-2} W/m^2) relative to field nauplii, further indicating a basic shift

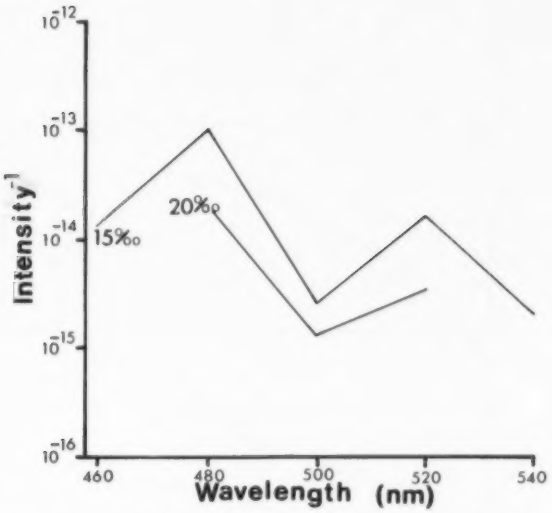

Fig. 1. Action spectrum for positive phototaxis of stage II dark-adapted *Balanus improvisus* nauplii: the reciprocal of the intensity (quanta/m^2/sec) inducing a positive phototaxis 10% above a predicted random response is plotted for nauplii at 15, and 20‰ *S*; thresholds of response were determined by testing 35–70 nauplii through a range of seven intensities at each wavelength.

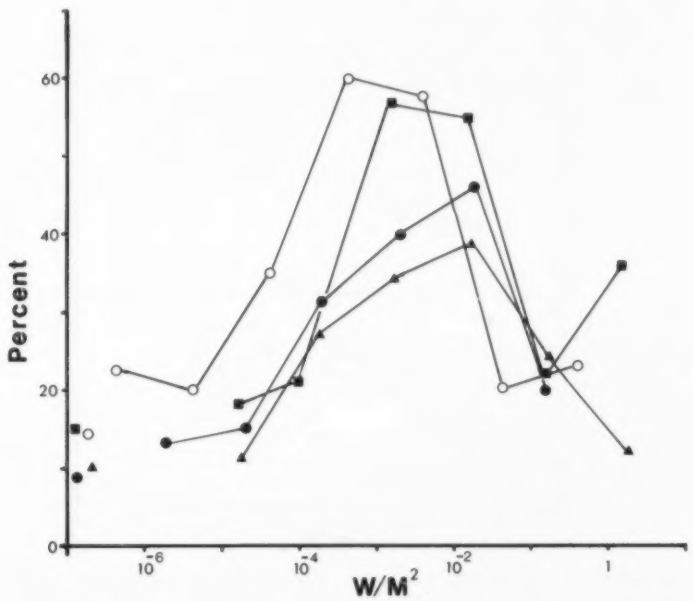

Fig. 2. The comparative positive phototactic response of laboratory-hatched and plankton-caught stage II dark-adapted *Balanus improvisus* nauplii to a 480-nm light stimulus at different intensities: the response of plankton-caught nauplii at 20 °C, 15‰ *S* (○) represents results from Lang *et al.* (1979a); response of laboratory-hatched nauplii (20 °C) at 15‰ *S* (●), 20‰ *S* (■), and 30‰ *S* (▲) are present results; to allow a direct comparison between studies, percent phototaxis is based on a directional response ±15° of the light stimulus (see text).

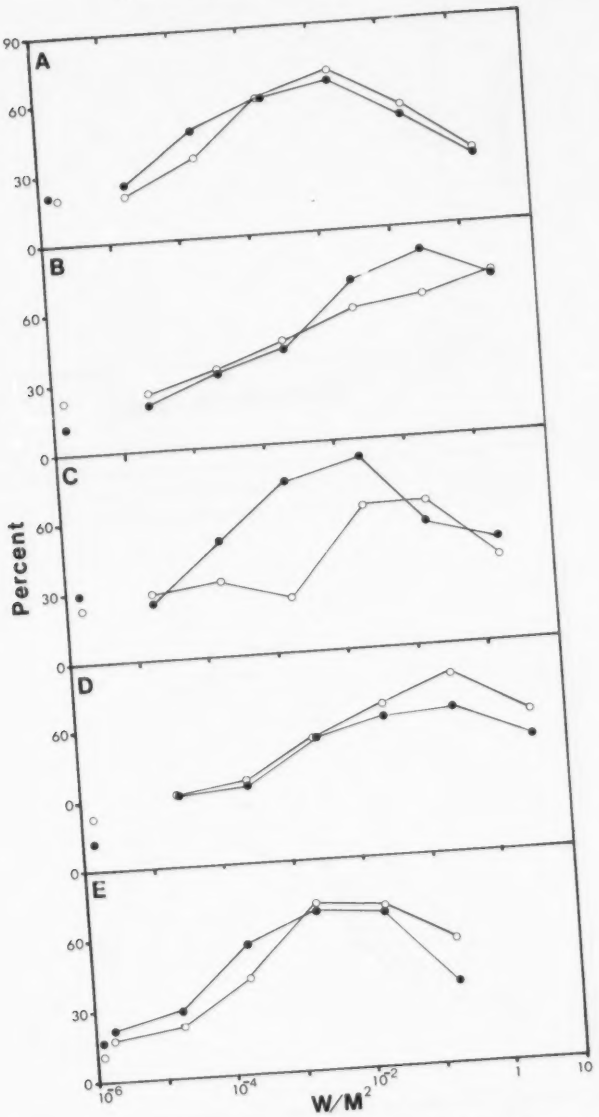

Fig. 3. Percent positive phototaxis of fed and 24-h starved stage II *Balanus improvisus* nauplii: A, dark-adapted nauplii at 30‰ *S*; B, light-adapted nauplii at 30‰ *S*; C, dark-adapted nauplii at 20‰ *S*; D, light-adapted nauplii at 20‰ *S*; E, dark-adapted nauplii at 15‰ *S*; ●, fed nauplii; ○, starved nauplii; the number of naupliar paths analyzed is given in Table I.

in the intensity range of significant phototaxis. The sensitivity of laboratory nauplii to 480 nm light remains similar at the three salinities tested, although nauplii at 20‰ *S* generally exhibited higher percent responses.

The effect of 24-h starvation on phototaxis was evaluated at 15‰ *S* using dark-adapted nauplii and at 20, and 30‰ *S* using both light- and dark-adapted nauplii. Within each specific salinity/light-adaptation treatment, results represent direct paired comparisons using fed and starved nauplii from the same laboratory hatch. The response of starved and fed nauplii is similar in most cases.

At 30‰ *S*, dark-adapted groups exhibit nearly identical phototactic response (Fig. 3A, Table I). Starved light-adapted nauplii at 30‰ *S* (Fig. 3B, Table I) exhibit a nearly linear response to increasing light intensities with peak percent phototaxis occurring at the highest intensity tested (4.0 W/m^2). Fed nauplii show a relative decline in response at 4.0 W/m^2 with peak response occurring between 10^{-2} to 10^{-1} W/m^2.

The most pronounced difference between fed and starved animals is seen with dark-adapted nauplii at 20‰ *S* (Fig. 3C, Table I). Starved nauplii are significantly less responsive to lower light intensities, but have responses similar to fed nauplii above 10^{-1} W/m^2. Starved light-adapted nauplii at 20‰ *S* show no difference in phototaxis at lower light intensities relative to fed nauplii, but may be slightly more responsive above 10^{-1} W/m^2 (Fig. 3D, Table I).

At 15‰ *S*, fed dark-adapted nauplii appear to be less responsive at the highest intensity (0.25 W/m^2) and more responsive below 10^{-3} W/m^2 relative to starved nauplii (Fig. 3E). These differences are slight, however, and both groups exhibit similar patterns of phototaxis.

Swimming speed of field nauplii, when illuminated with only substage (830 nm) light (i.e. undirected 'control' response), is about 1.5 mm/sec MLV for light- and dark-adapted nauplii at 15‰ *S*, 20 °C (Lang *et al.*, 1979a) and 1.8 mm/sec at 30‰ *S*, 20 °C (unpubl. results).

Laboratory-hatched dark-adapted nauplii at 15‰ *S* have a control MLV of about 1.1 mm/sec; light- and dark-adapted nauplii at 20‰ *S* have a control MLV of about 1.6 mm/sec; dark-adapted nauplii at 30‰ *S* have a control MLV of 1.8 mm/sec. Light-adapted nauplii at 30‰ *S*, however, exhibit a low control MLV of 1.4 mm/sec and consistently reduced swimming speeds also persist in this group during light stimulation (Table I). With the exception of this last group (light-adapted, 30‰ *S*), MLV of field and laboratory nauplii are similar.

Field stage II nauplii increase MLV in response to light stimulation (Lang *et al.*, 1979a). Dark-adapted nauplii exhibit a maximal MLV at intermediate light intensities which also induce maximal phototaxis. On the other hand, light-adapted nauplii exhibit a maximal MLV at the highest light intensities tested, irrespective of strength of directional response.

Analysis of MLV for laboratory hatched nauplii (Table I) indicate similar responses. Fed light-adapted nauplii exhibit maximal MLV at the highest light in-

TABLE I

Mean linear velocity (MLV) and χ^2 comparison of directional orientation for stage II *Balanus improvisus* nauplii (laboratory) responding to a 3.5-sec 480-nm light stimulus of varying intensity (see text): the χ^2 value is based on a comparison of observed directional distributions with a theoretical uniform distribution (Batschelet, 1965); *, significant ($P \leq 0.05$) non-random responses; homogeneous subsets for MLV were determined by a Duncan's multiple range test ($\alpha = 0.05$); control results represent the swimming response of nauplii for 3.5 sec with substage 830 nm illumination only; the sample number (n) represents the number of naupliar paths computer analyzed at each condition.

	S, 20‰							
	Fed				Starved			
Intensity (W/m^2)	n	χ^2	MLV (mm/sec)	Subset	n	χ^2	MLV (mm/sec)	Subset
Dark-adapted								
2.5	25	16*	1.98	AB	39	15*	1.70	AB
10^{-1}	27	33*	1.87	ABC	33	49*	1.93	A
10^{-2}	68	212*	1.82	ABC	75	118	1.78	AB
10^{-3}	30	71*	2.05	A	33	13*	1.54	BC
10^{-4}	39	35*	1.57	C	34	11	1.39	C
10^{-5}	34	9	1.62	ABC	35	6	1.70	AB
Cont.	34	5	1.62	BC	33	6	1.69	AB
Light-adapted								
4.0	27	29	2.47	A	17	26*	2.51	A
10^{-1}	26	39*	1.70	BC	25	64*	2.44	A
10^{-2}	63	73*	1.80	B	51	87*	1.47	B
10^{-3}	31	26*	1.52	C	27	29*	1.23	B
10^{-4}	29	7	1.51	C	33	7	1.26	B
10^{-5}	30	10	1.54	C	33	8	1.53	B
Cont.	26	12*	1.64	BC	26	5	1.25	B

	S, 30‰							
	Fed				Starved			
Intensity (W/m^2)	n	χ^2	MLV (mm/sec)	Subset	n	χ^2	MLV (mm/sec)	Subset
Dark-adapted								
2.5	57	12*	1.84	A	46	18*	1.75	B
10^{-1}	65	50*	2.01	A	49	53*	2.02	A
10^{-2}	67	174*	2.04	A	87	182*	2.08	A
10^{-3}	94	117*	1.82	A	91	105*	1.54	BC
10^{-4}	67	50*	2.05	A	52	17*	1.49	BC
10^{-5}	76	6	1.83	A	64	3	1.50	BC
Cont.	59	6	1.81	A	66	3	1.43	C
Light-adapted								
4.0	39	72*	1.61	A	40	78*	2.00	A
10^{-1}	38	108*	1.54	A	40	62*	1.55	B
10^{-2}	69	133*	1.29	B	73	83*	1.13	C
10^{-3}	27	12*	1.15	B	39	23*	1.13	C
10^{-4}	37	8	1.26	B	43	10	1.22	C
10^{-5}	31	6	1.16	B	32	5	1.20	C
Cont.	34	7	1.38	AB	34	6	1.24	C